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UNIVERSITY OF ALBERTA

PARENTAL INVESTMENT IN BROOD DEFENCE BY WILLOW PTARMIGAN

BY

BRETT K. SANDERCOCK

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND

RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR

THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1991

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled PARENTAL INVESTMENT IN BROOD DEFENCE BY WILLOW PTARMIGAN submitted by BRETT K. SANDERCOCK in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Dr. Susan J. Hannon (Supervisor)

Dr. Jan O. Murie

Dr. Joseph S. Nelson

Dr. Marcia L. Spetch

DATE: August 9/91

DEDICATION

I dedicate the efforts of my Master of Science thesis to my parents and brother. I credit the encouragement of my parents for giving me an early interest in biology. Their own academic achievements in zoology have given me goals which I continue to strive towards. I thank my brother for his strong disinterest in biology because he helps me to put my interests in a broader perspective.

ABSTRACT

I investigated parental investment in brood defence by willow ptarmigan (*Lagopus l. alexandrae*). I tested the importance of offspring number on brood defence. I also examined variation in brood defence with changes in annual conditions, offspring age and characteristics of the parents.

I compared the effect of past investment in the clutch and future benefit of brood size on the parental defence of offspring. I manipulated offspring number so that females with different clutch sizes had the same brood size and females with the same clutch size had different brood sizes. I predicted that ptarmigan defence should be unaffected by past investment in the clutch but should increase with the future benefit of brood size. Clutch size did not affect defence and unexpectedly, neither did brood size. I present three testable hypotheses based on parental investment, life history and offspring mobility that may explain why ptarmigan defence was unaffected by brood size. Only the offspring mobility hypothesis is consistent with the defence of offspring by ptarmigan, altricial birds and fish.

Characteristics of the offspring and parents appeared to be the most important factors affecting brood defence in willow ptarmigan. Annual conditions did not affect defence. Defence declined after the young fledged, probably because offspring vulnerability had declined. The parent's past experience with the observer, potential for other nesting attempts and the reproductive value of the offspring did not affect defence. Females gave stronger defence than males, possibly because their plumage put them at less risk of predation or because they had higher certainty of parentage in the young. Ptarmigan body condition and reproduction in future breeding seasons did not appear to be important.

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My supervisor, S. Hannon, gave me excellent guidance during my stay at the University of Alberta. The valuable data and unpublished manuscripts that she shared with me has enhanced my thesis. Her insightful criticism of the many proposals and papers that crossed her desk helped me avoid faulty logic and achieve greater clarity. The time and effort she exerted on my behalf has extended far beyond any obligation and I am greatly in her debt.

I was fortunate to have capable assistance during my fieldwork in the Chilkat Pass, British Columbia. My assistants, H. Dundas and S. Lee worked many long hours in unfavorable field conditions and I owe the quality of my behavioral data to their meticulous observations. C. Schuppli and G. Dobush generously integrated their research projects with my work. By sharing resources, I was able to accomplish much more than would have otherwise been possible. G. Dobush gave me a valuable introduction to techniques for collecting behavioral data and capturing the most wily willow ptarmigan. R. Gruys, S. Hannon, I. Jönsson, S. More, K. Murie, A. Paul, and J. Schieck all helped me band and radio-track a large sample of willow ptarmigan. I also thank the Kluane Lake Research Station, Blanchard River Highway Camp and Pleasant Camp Customs Station for their logistical support.

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CHAPTER 1: THESIS INTRODUCTION

Parental investment theory has been a useful framework for investigating the factors that affect avian defence of young. Trivers (1972) defined parental investment as: "any investment by the parent ... that increases the offspring's chance of surviving ... at the cost of the parent's ability to invest in other offspring". Defense of young differs from other components of parental care in that inappropriate defense may have a large cost. In an encounter with a predator, a parent may be killed if its defense is strong but the young may be eaten if its response is weak (Montgomerie and Weatherhead 1988). Further, a parent cannot defer defense if the young are threatened but can postpone feeding and brooding under most conditions. Thus, defense should indicate the parents' willingness to invest in their brood more effectively than feeding or brooding.

There are few records of predators killing birds while they defend their young (but see Brunton 1986), probably because predator encounters are rare and because predator avoidance should be a strong selection pressure (Montgomerie and Weatherhead 1988). The benefits of strong defence have been better documented. Correlations between offspring number and defence scores (Pedersen and Steen 1985; Wiklund 1990) may demonstrate that strong defence improves offspring survival but a parent may also invest more strongly in a large brood. Several studies have shown that the initial defence of birds with nests that subsequently failed (Andersson et al. 1980; Greig-Smith 1980; Blancher and Robertson 1982; Weatherhead 1990) is weaker than the defence of birds that successfully reared their nests to independence. This appears to be evidence for the benefit of strong defence. However, if parents that give weak defence also have poor ability to feed or brood offspring, nests may have failed for other reasons and later been destroyed by scavengers. The best evidence for the benefit of strong defence comes from hormonal manipulations of brood defence. Pedersen (1989) was able to elicit strong defence by implanting prolactin in female willow ptarmigan and found that aggressive

females had larger broods at fledging.

The objective of my research was to examine the factors affecting brood defence of willow ptarmigan. In Chapter 2, I examine the effect of offspring number on ptarmigan defence. I manipulated brood size to separate two factors that were correlated for the parents: past investment in the clutch and future benefit of brood size. I also tested the assumptions that egg and parent quality were similar for all clutches. In Chapter 3, I compare the brood defence of willow ptarmigan in the Chilkat Pass, British Columbia to previous work on red grouse and willow ptarmigan in Europe. I also examine changes in defence among years and with offspring age. I describe the influence of parental characteristics such as body condition, plumage and certainty of parentage on defence.

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CHAPTER 2: THE EFFECT OF PAST INVESTMENT AND FUTURE BENEFIT ON BROOD DEFENCE BY WILLOW PTARMIGAN: AN EXPERIMENTAL APPROACH[1]

Introduction

Parental investment in care of young should be determined by the future expected benefit of the young rather than the parent's past investment (Dawkins and Carlisle 1976; Boucher 1977). Parents that base care of young on past investment and not future benefit (the Concorde fallacy, Dawkins 1976) may risk loss of future attempts at reproduction. However, if past investment is a good predictor of future benefit (Carlisle 1985; Coleman et al. 1985), parental investment decision rules may be influenced by past investment and still be optimal.

Despite a considerable body of literature in this area, there have been few empirical tests of these predictions. For two reasons, our understanding of the relative importance of past investment and future benefit is limited. The first difficulty is that the two factors are hard to separate for comparison because they are often positively correlated (eg. Weatherhead 1979; 1982). Second, because parental care is considered adaptive, usually ultimate hypotheses are suggested and proximate constraints are overlooked.

Past reproductive investment can be measured in birds by clutch size because the costs of egg production and incubation increase with the number of eggs a female lays (eg. Robertson and Biermann 1979; Windt and Curio 1986). Eggs of precocial birds have a high energy content (Carey et al. 1980) and the cost of forming eggs is 21-30% of the daily energy intake of most Galliformes (King 1973). The basal metabolic cost of incubation (Biebach 1981; Haftorn and Reinertsen 1985; Moreno and Carlson 1989), the energy required to rewarm the clutch after an incubation break (Gabrielsen and Steen 1979; Vleck 1981) and the length of the incubation period (Jones 1987; Coleman and

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[1] A version of this chapter has been submitted for publication to Behavioral Ecology and Sociobiology

Whittall 1988; Smith 1987) are all correlated positively with clutch size. A large clutch may give an incubating parent a homeothermic advantage if the embryos generate heat (Clark 1984) but it is unlikely that this would offset the above costs. Future benefit for females can be measured as brood size, assuming that more young will recruit to the breeding population from large broods (eg. Wiklund 1990).

Past investment and future benefit are more difficult to measure for males. Males can have a large past investment in territorial defence or nest building, but it is unclear if these costs are correlated with the female's clutch size. Future benefit may not be correlated with brood size for males if extra-pair copulations reduce their confidence of paternity.

I manipulated offspring number to compare the effects of past investment in the clutch and future benefit of brood size on the parental defence of willow ptarmigan (*Lagopus l. alexandrae*). Willow ptarmigan are a monogamous grouse with a circumpolar distribution. The females lay initial clutches of 5 to 11 eggs (Hannon et al. 1988) in shallow scrapes on the ground. Intraspecific nest parasitism is rare in willow ptarmigan (Martin 1984, Hannon unpub. data) and a clutch is the investment of one hen. If the clutch is lost, birds can renest, but only one brood is produced per season. The precocial young leave the nest at hatch and are not fed by the parents. Ptarmigan chicks are nourished by a yolk sac until 2-3 days of age (Bergerud 1970) and are able to maintain homeothermy by six days of age (Aulie 1976). Willow ptarmigan are unique among grouse as both mates defend the young after hatch (Wittenberger 1978).

Previous studies of past investment or future benefit and their effect on parental care have used altricial birds or fish. I examined a bird with precocial young and I made two predictions: 1) if past investment is greater for large clutches, defence should be unaffected by clutch size because defence based on past investment is nonoptimal (Dawkins and Carlisle 1976; Boucher 1977), and 2) if more young recruit from a large brood and give the parent greater

fitness, defence should increase with brood size because the future benefit is greater.

Study area and methods

I conducted this study at the Chilkat Pass, in northwestern British Columbia, Canada (59°50'N, 136°30'W) during the breeding seasons of 1989 and 1990. Willow ptarmigan have been studied at this site since 1979. The study area is covered by a mixture of willow (*Salix* spp.) and birch (*Betulosa glandulosa*) shrubs and has been described in detail elsewhere (Weeden 1960; Hannon 1984; Gruys 1991).

Predator encounters with ptarmigan nests and broods are rarely observed. Potential predators of chicks observed on the study area include: red foxes (*Vulpes vulpes*), short-tailed weasels (*Mustela erminea*), mew gulls (*Larus canus*), northern harriers (*Circus cyaneus*), short-eared owls (*Asio flammeus*) and common ravens (*Corvus corax*).

Willow ptarmigan were captured with noosing poles and ground nets (Hannon 1983) in early spring before laying began. Each bird was banded with a unique color combination and sex was determined by plumage. Females were collared with small (<20g) radio-tags in order to find their nests and broods. Females were located by telemetry every second day during laying in order to find nests. When a nest was found, the female was flushed to measure clutch size and the nest was marked with yellow flagging tape at a distance of greater than 10 m. Marking of this sort has no effect on the ability of predators to detect nests (Hannon unpub. data). After laying was completed, the female was flushed to count the final clutch size, and in some cases, to float the eggs to estimate stage of incubation (after Westerkov 1956). The nest was not disturbed again until the end of incubation (approximately 21 days, Schieck 1988). In determining past investment in clutch size, I counted eggs that did not hatch as equivalent to eggs that produced chicks. All chicks were individually marked with patagial wing tags at hatch (Hannon et al. 1990).

Broods were manipulated on the day of hatch to separate the effects of

past investment in the clutch and the future benefit of the brood. Only broods from first nests were used, as past investment was often unknown for females that renested. Approximately the same number of chicks were added to or removed from each brood and the broods were within the range of natural brood sizes (5-11 chicks, Hannon et al. 1988). The parents were left to acclimate to the change in brood size overnight before I returned to record defence the next day.

In my experiments, I assumed all chicks survived until I recorded parental defence behavior. I estimated the minimum number of chicks that were present from brood counts in the two weeks after hatch. Young ptarmigan chicks are very cryptic and counts of brood size are not efficient until the chicks fledge at 10-12 days of age. This method gives a maximum estimate of chick loss if mortality occurs before the chicks fledge. I examined the fate of the chicks I moved to other broods in 1989 and 1990 by recovering wing tags from yearlings and fledglings.

In experiment 1, I tested parental defence of broods where past investment was different and future benefit was the same. Two chicks were added to or removed from broods from clutches of 6 or 10 eggs to produce broods of 8 chicks. To control for manipulation disturbances, I exchanged two chicks between control broods from 8 egg clutches.

In experiment 2, I tested parental defence of broods where past investment was the same and future benefit was different. Three chicks were added to or removed from broods from clutches of 7,8 or 9 eggs to produce broods ranging from 4 to 12 chicks. The controls were the same as above but also included broods from clutches of 7 and 9 eggs.

I scored parental defence once only for each brood to avoid habituation. My assistant and I located each brood with radio telemetry and approached until one parent reacted. We recorded defence for 3 minutes in response to the taped distress call of a day old chick. Chick calls are pure tones (Wike and Steen 1987) and it is unlikely that parents recognize their own chicks. Our

activity simulated a natural predator because the parents perceived us to be a threat and acted more aggressively than birds without broods.

Each observer recorded the focal behavior of one parent. We continuously recorded three measures of defence behavior: postures, vocalizations and distance from the observer. I subjectively estimated the parent's risk of predation in these behaviors. High risk behaviors were usually observed only at the start of an encounter but continued if the parent's defence was strong. Low risk postures included sitting or standing, moderate risk postures included walking and running, and high risk postures included wing dragging, shaking the body and flying in short, active hops. I considered vocalizing or remaining less than 5 m from the observer to be high risk.

I used nonparametric tests for statistical comparisons when sample size was small or the underlying distribution was not normal. All tests were performed using procedures from SAS (SAS Institute, 1987). All tests were two-tailed and considered significant at probability levels less than 0.05.

Results

Tests of assumptions

There were several assumptions in my study that were important for interpretation of my experimental results: 1) that age of parent did not affect clutch size; 2) that egg quality was unaffected by clutch size; 3) that clutch and brood size were good measures of past investment and future benefit; 4) that all chicks survived overnight until I recorded defence; and 5) that conditions in the years of my study were similar. I used data collected in the Chilkat Pass from 1985-1990 to test the first three assumptions.

Age Class of Parent. Female age could have differed among treatments in experiment 1 if older females laid larger clutches. Of the parents I observed, 58.6% (n=29) of the females and 42.3% (n=26) of the males were yearlings. Mean clutch size of yearling and adult females was different in 1985-1988 (Hannon unpub. data) but was not for the females I observed in 1989-1990 (yearlings: 8.00±1.17 SD eggs, n=17; adults: 8.50±1.09 SD eggs, n=12; t=-1.16,

P=0.25). The numbers of yearlings and adults of both sexes were balanced among the treatments in both experiments.

Egg quality. Egg quality could have varied among treatments in experiment 1 if there was a tradeoff between clutch size and egg quality. Eggs of poor quality could be smaller, produce lighter chicks or fail to hatch. Egg size varies little among willow grouse (*Lagopus l. lagopus*) clutches of different size (Myrberget 1977; Erikstad et al. 1985). I found no difference in mean chick weight at hatch among clutches of different size (Table II-1). The clutch size distribution of nests with partial failure (from unfertilized eggs or eggs that failed to hatch, n=70 nests) was not different from the distribution of nests with no partial failure (n=87 nests, χ^2=2.75, P>0.50). Thus, I conclude that egg quality was the same for all clutch sizes.

Clutch size and brood size as measures of past investment and future benefit. Length of incubation and female body condition at hatch are two measures of a female's past investment. To estimate length of incubation, I used clutches found during laying and I assumed that females began incubation on the penultimate egg (Schieck 1988). There was no difference in length of incubation among clutches of different size (Table II-1). Body mass was not affected by clutch size for females captured 1-4 days after hatch (Table II-1). Although neither measure of incubation cost increased with clutch size, a female's past investment probably increased with clutch size through egg formation costs.

Future benefit will increase with brood size if more young recruit to the breeding population from large broods. Martin and Hannon (1987) showed that fledging success is a good measure of recruitment because more recruits return from large broods of fledglings. In unmanipulated broods, the number of fledged chicks was correlated positively with the number of hatched chicks (n=77 nests, Spearman r=0.51, P<0.0001). For almost all initial brood sizes, all the chicks of some pairs successfully fledged. Brood size was a good measure of future benefit because the correlation between hatched and fledged chicks

Table II-1. Chick weight at hatch, length of incubation and adjusted female body mass for first nests of 6-10 eggs[a]. All data are from 1985-1990. Means are given ±1SD. Sample size of nests and females are within parentheses.

Egg No.	Chick Weight at Hatch (grams)	Length of Incubation (days)	Body Mass at Hatch[b] Adult (grams)	Yearling (grams)
6	14.5 ± 1.3 (10)	21.0 ± 1.4 (4)	- (0)	404.4 ± 24.0 (6)
7	14.5 ± 1.0 (23)	20.6 ± 0.9 (17)	412.0 ± 31.0 (5)	405.9 ± 35.5 (14)
8	14.5 ± 1.2 (39)	21.0 ± 0.9 (25)	414.1 ± 13.1 (7)	399.1 ± 18.5 (16)
9	14.9 ± 1.2 (48)	20.6 ± 0.8 (35)	431.8 ± 28.8 (11)	394.7 ± 23.5 (9)
10	14.6 ± 0.9 (24)	20.8 ± 0.9 (18)	413.6 ± 25.5 (4)	416.5 ± 21.0 (5)
F	0.87	0.97	1.13	0.69
P	0.48	0.43	0.36	0.60

[a] Clutches of 5 and 11 eggs were not used in brood size manipulations and were not included here because of insufficient data.
[b] Body mass adjusted for wing length by analysis of covariance.

was highly significant and because all pairs may have the possibility of 100% fledging success.

Chick survival. Chick loss between hatch and the day I recorded defence would have affected both experiments. Control or addition broods would have changed treatment group if 2 or more chicks died before the chicks were one day old. Chick loss was less than 2 chicks in 72.4% (n=29) of the broods. Brood counts after hatch gave a maximum estimate of chick loss and the actual chick survival until I recorded defence was probably higher. However, if I excluded broods where 2 or more chicks were lost, my conclusions in the analyses below were unchanged.

If parents had recognized their young and excluded unfamiliar chicks, chicks that were moved to foster broods at hatch could have had low survival. I moved 18.7% (n=150) of the chicks I tagged in 1990 and 30% (n=20, Binomial, P=0.09) of the wing tags in recaptured fledglings in 1990 were from birds moved as chicks. I moved 17.5% (n=137) of the chicks I tagged in 1989 and 37.5% (n=8, Binomial, P=0.12) of the wing tags I recovered from yearlings in 1990 were from birds moved as chicks. Thus, moving chicks did not decrease their survival to fledging or to recruitment.

Year effects. The proportion of hens giving distraction displays has varied between years in studies of willow (Pedersen and Steen 1985) and red grouse (*Lagopus l. scoticus*, Hudson and Newborn 1990), possibly as a function of breeding density, seasonal phenology or predation pressure. The density of breeding pairs increased from 17.9 pairs/km^2 in 1989 to 23.4 pairs/km^2 in 1990. Mean clutch size of all females on the study area was significantly smaller in 1990 than 1989 but was not different for the females in my experiments (Table II-2). Date of hatch was significantly earlier in 1989 than 1990 but only by 2 days (Table II-2). In both years, at least 85% of the successful first nests hatched within one week. The predation rate on first nests was high in both years and not significantly different (Table II-2). Every parent gave a display and I observed no obvious differences in defence

Table II-2: Clutch size, date of hatch and predation rate for first nests in 1989 and 1990. Means are give ±1SD. Sample sizes of first nests are within parentheses.

Year	Clutch size of All Females	Clutch size of Study Females	Date of hatch (Julian date)[a]	Predation of 1st Nests (% nests lost)
1989	8.34 ± 1.07 (29)	8.33 ± 1.23 (12)	176.25 ± 1.82 (12)	66.7% (42)
1990	7.73 ± 1.43 (57)	8.81 ± 1.11 (17)	174.18 ± 2.58 (17)	77.3% (88)
t	2.01	0.49	2.39	
χ^{2b}				0.52
P	0.048	0.63	0.02	0.40

[a] Day 175 = June 24
[b] χ^2 with Yate's correction

behavior between 1989 and 1990. I pooled defence data from both years in the subsequent analyses because clutch size, date of hatch and predation pressure were similar between years.

Experiment 1: Past investment variable and future benefit equal

Past investment in the clutch did not affect the defence level of females or males. There was no difference among treatments (Fig. II-1) in the proportion of time parents spent in high risk postures (Kruskall-Wallis χ^2 approximation, ♀♀ χ^2=4.67, P=0.56; ♂♂ χ^2=4.23, P=0.12), vocalizing (♀♀ χ^2=0.75, P=0.69; ♂♂ χ^2=0.03, P=0.99) or less than 5 m from the observer (♀♀ χ^2=1.17, P=0.56; ♂♂ χ^2=0.77, P=0.68). Females and males did not differ in the proportion of time they spent in high risk postures (Mann-Whitney, U=1.03, P=0.31) or less than 5 m from the observer (U=2.27, P=0.13) but there was a trend for males to spend less time vocalizing than females (U=3.68, P=0.055).

Experiment 2: Future benefit variable and past investment equal

The future benefit of brood size did not affect the defence level of females or males. There was no difference among treatments (Fig. II-2) in the proportion of time parents spent in high risk postures (♀♀ χ^2=4.73, P=0.09; ♂♂ χ^2=0.14, P=0.93), vocalizing (♀♀ χ^2=1.27, P=0.53; ♂♂ χ^2=1.33, P=0.51) or less than 5 m from the observer (♀♀ χ^2=2.03, P=0.36; χ^2=0.58, P=0.75). Females and males did not differ in the proportion of time they spent in high risk postures (Mann-Whitney, U=0.13, P=0.72) or less than 5 m from the observer (U=0.98, P=0.32). Males spent a significantly lower proportion of time vocalizing than females (U=4.75, P=0.029).

Discussion

Past investment and defence

The Concorde fallacy implies that a parent's options are to base investment on *either* past investment *or* future benefit. This is misleading because a parent may also base investment on *neither* (this study) or *both* (Coleman et al. 1985) of these components. Thus, several studies have concluded that parents did not base defence on past investment if defence varied with brood size

Fig. II-1. Experiment 1: The proportion of time spent in defence behavior versus past investment in clutch size. The expected benefit of brood size was 8 chicks in all treatments. Each point is a $\bar{x}$±1SE. Females: all treatments n=3; males: 6 egg clutches n=2, 8 or 10 egg clutches n=3. The sample sizes differ because one female was not accompanied by her mate.

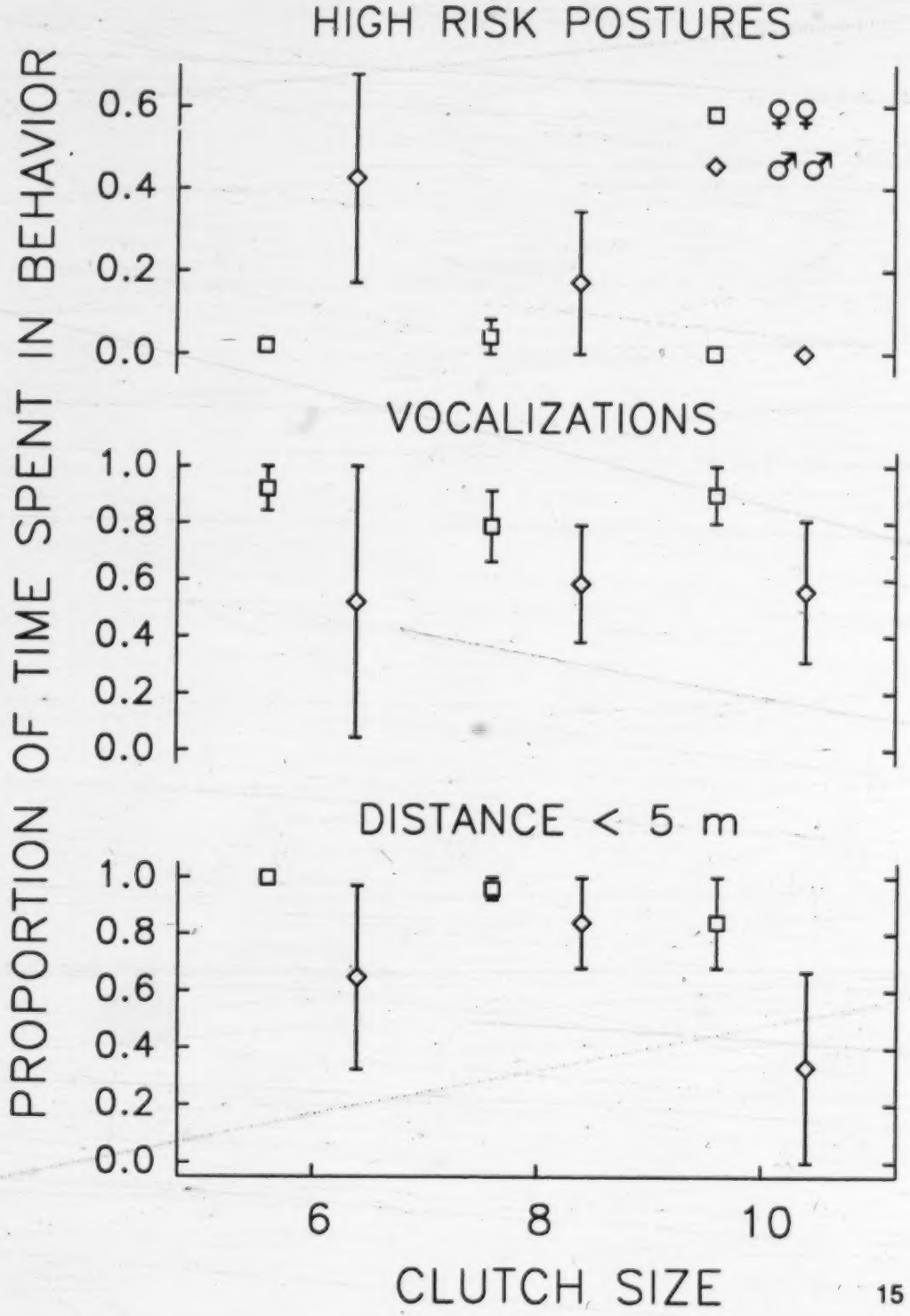
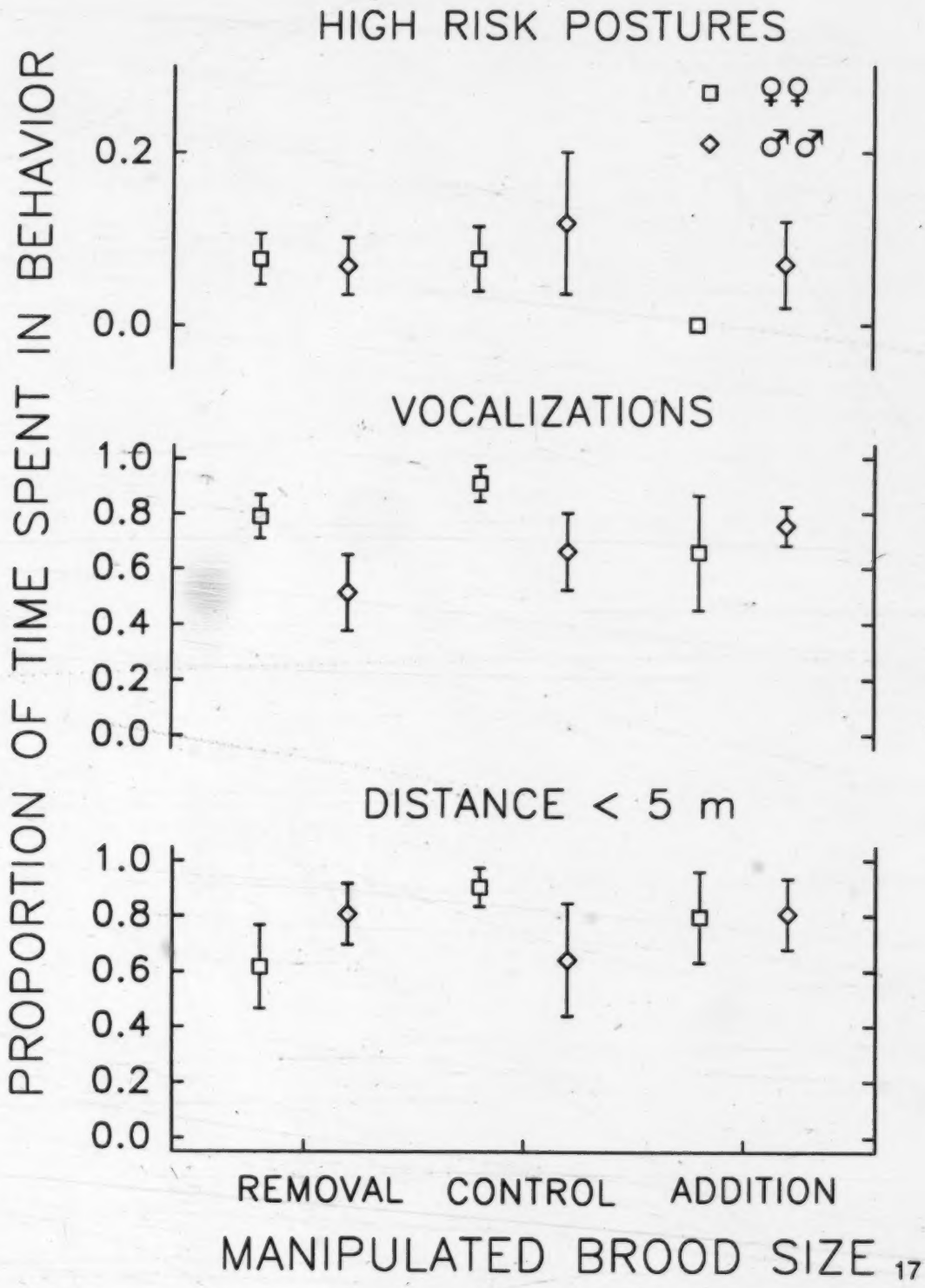

HIGH RISK POSTURES
VOCALIZATIONS
DISTANCE < 5 m
PROPORTION OF TIME SPENT IN BEHAVIOR
0.0
0.2
0.4
0.6
0.8
1.0
♀♀
♂♂
6
8
10
CLUTCH SIZE

Fig. II-2. Experiment 2: The proportion of time spent in defence behavior versus expected benefit of brood size. Past investment in clutch size was 7,8 or 9 eggs in all treatments. Each point is a $\bar{x}\pm 1SE$. Females: removal $n=10$, control $n=7$, addition $n=6$; males: removal $n=9$, control $n=6$, addition $n=6$. The sample sizes differ because two females were not accompanied by their mates.


HIGH RISK POSTURES
♀♀
♂♂
0.2
0.0
VOCALIZATIONS
1.0
0.8
0.6
0.4
0.2
0.0
DISTANCE < 5 m
1.0
0.8
0.6
0.4
0.2
0.0
PROPORTION OF TIME SPENT IN BEHAVIOR
REMOVAL
CONTROL
ADDITION
MANIPULATED BROOD SIZE

(Robertson and Biermann 1979; Carlisle 1985; Windt and Curio 1986). Although consistent with the Concorde fallacy as stated, this conclusion is erroneous because past investment was the same for all parents.

Few studies have attempted to examine the effect of past investment where future benefit was similar or to manipulate past investment. Weatherhead (1979) compared the defence of male and female savannah sparrows (*Passerculus sandwichensis*). He suggested females committed the Concorde fallacy because they had more past investment (in egg laying, incubation and feeding) and stronger defence than males. He assumed future benefit was equal for both sexes, but recent work has shown that extra-pair copulations in monogamous species (eg. Westneat 1987a, 1987b) may reduce confidence of paternity for a male. Weatherhead (1982) manipulated past investment in red-winged blackbirds (*Agelaius phoeniceus*) by exchanging broods of different ages. Defence varied with the amount of past investment in incubation but females could have used length of incubation to estimate offspring age. If parents used confidence of paternity or offspring age to evaluate future benefit, past investment and future benefit would have been correlated.

Coleman et al. (1985) successfully controlled for future benefit in bluegill sunfish (*Lepomis macrochirus*) and found defence was greater for males with more past investment in the brood. This result was consistent with committing the Concorde fallacy but the authors suggested that defence could still be optimal if the parents used past investment to predict future benefit. Their key assumption was that costs of reproduction were present. If costs are present, the size of a parent's past investment may limit its future reproduction in a predictable way. Correlative and manipulative studies of offspring number in birds (reviewed in Partridge 1989), however, have not always detected a cost of reproduction.

The effect of past investment on willow ptarmigan defence of young

I concluded that quality of the parents and eggs did not vary among treatments

in experiment 1 because yearlings and adults laid similar numbers of eggs and because clutch size had no effect on mean chick weight at hatch or partial clutch failure. Willow ptarmigan have negligible body reserves entering breeding (Thomas 1982) and egg production costs should be proportional to clutch size if females may spend more time foraging to lay a large clutch. I detected no cost of incubation as length of incubation and female body weight at hatch were unaffected by clutch size. Body weight at hatch may be misleading as a measure of past investment, however, because females in poor condition after laying can compensate by taking more breaks during incubation (Erikstad 1986). Egg production and incubation costs are important for other birds (Haftorn and Reinertsen 1985; Coleman and Whittall 1988) and past investment should increase with clutch size for ptarmigan as well.

My conclusions from experiment 1 are tentative because the sample size is small but the trend for males to vocalize less than females demonstrates that the data should have had sufficient resolution to show differences among treatments. Clutch size had no effect on willow ptarmigan defence of young in experiment 1. Thus, my study is one of the first to separate future benefit from past investment and support the prediction (Dawkins and Carlisle 1976; Boucher 1977) that parents should avoid basing parental care on past investment in their offspring.

Future benefit and defence

Defence by parents in response to manipulated brood size has been examined in four altricial birds and three fish. These studies all attempted to keep past investment (usually measured as offspring age) constant among treatments. Although the stimuli and measures of defence differed, the results of these studies are remarkably consistent. The defence level of stonechats (*Saxicola torquata*, Greig-Smith 1980), great tits (*Parus major*, Windt and Curio 1986) and female merlins (*Falco columbarius*, Wiklund 1990) changed relative to the number of nestlings. The proportion of goldfinch parents (*Carduelis tristis*, Knight and Temple 1986) changing their call rates covaried with the addition or

removal of nestlings. Defence was also found to be proportional to brood size in female cichlids (*Aequidens coeruleopunctatus*, Carlisle 1985), male bluegill sunfish (Coleman et al. 1985) and male smallmouth bass (*Micropterus dolomieui*, Ridgway 1989).

The effect of future benefit on willow ptarmigan defence of young

Brood size had no effect on willow ptarmigan defence of young in experiment 2. The lack of effect of future benefit is inconsistent with all previous empirical evidence. I present two ultimate and one proximate explanation for this pattern and offer suggestions for how these hypotheses might be tested in further studies.

H1: The residual reproduction hypothesis. The life history of birds may affect their defence behavior. Adult survivorship is low for *r*-selected birds and breeding opportunities in future seasons may be uncertain (a low residual reproductive value, Pianka and Parker 1975). This hypothesis predicts that birds with low survivorship should defend young from every reproductive attempt strongly without regard to offspring number.

Willow ptarmigan have a low residual reproductive value. They have many characteristics of an *r*-selected species including: high annual mortality (50-60%), no delayed maturity and a large clutch size (Hannon and Smith 1984). Defence may have been unaffected by brood size in this study because all parents were uncertain about future breeding and defended their young strongly. This prediction fails to explain why the defence of small passerines such as great tits covaried with brood size (Windt and Curio 1986) when their survivorship is low and age-independent (Bulmer and Perrins 1973).

H2: The shared parental investment hypothesis. If parental care is provided to the whole brood and not sequentially to individual offspring, there may be proximate constraints on a bird's ability to count their young. In birds, all young in a brood usually benefit equally from incubation, brooding and defence whereas food brought to the nest or a parent's vigilance may be monopolized by individual offspring (Lazarus and Inglis 1986). Thus, feeding

and vigilance may provide a mechanism for parents to estimate offspring number. This hypothesis predicts that defence should be unaffected by offspring number if parental care is not provided to individual young.

In willow ptarmigan, defence is shared equally by the young because parents defend an area where scattered chicks are concealed. All young should benefit equally from brooding unless brood size exceeds the female's considerable brooding capacity. Thus, defence may have been unaffected by brood size in this study because willow ptarmigan were unable to count and could not detect a change in brood size of 2-3 chicks. The difference between willow ptarmigan and altricial birds (Greig-Smith 1980; Knight and Temple 1986; Windt and Curio 1986; Wiklund 1990) is consistent with this hypothesis. It is unclear, however, why the defence of fish (Carlisle 1985; Coleman et al. 1985; Ridgway 1989) was proportional to brood size when their young benefitted equally from egg fanning and other components of fish parental care.

H3: The offspring mobility hypothesis. Parental defence may depend on whether the young are clumped or scattered during a predator encounter. If chicks are scattered, a predator cannot threaten the whole brood (Andersson et al. 1980) and defence should be independent of offspring number (Lazarus and Inglis 1986). This hypothesis predicts that defence should be affected by offspring number if the young are clumped but not if they can scatter.

Defence may have been unaffected by brood size in this study because the chicks scattered in all brood encounters. Studies of altricial birds and fish are consistent with this hypothesis because the parents defended offspring that were clumped in a nest (Greig-Smith 1980; Knight and Temple 1986; Windt and Curio 1986; Wiklund 1990) or egg mass (Coleman et al. 1985; Ridgway 1989). Carlisle (1985) did not describe the behavior of cichlid broods, but I assume the young were clumped as cichlid fry often school when threatened (Keenleyside 1979).

Predictions and Future Research

To test the residual reproduction hypothesis, offspring number should be

manipulated in birds that have survivorship on the extremes of the *r-K* continuum (Stearns 1976). For example, dabbling (tribe *Anatini*) and diving (tribe *Anserini*) ducks are associated, respectively, with *r* and *K*-selected life history traits (Eadie et al. 1988). This hypothesis predicts the defence of *r*-selected birds should be independent of offspring number whereas the defence of *K*-selected birds should be dependent on offspring number.

Both the shared parental investment hypothesis and the offspring mobility hypothesis predict that parental defence should increase with offspring number for altricial young in the nest and be unaffected by offspring number for precocial young that have left the nest. However, exclusive predictions can be made if a component of parental care (such as feeding) is not shared equally by the young and the young can scatter. In altricial birds, these conditions are met if parents provide food to young that have fledged and left the nest. In a few altricial birds, such as black-billed magpies (*Pica pica*, Redondo and Carranza 1989) and northern harriers (*Circus cyaneus*, F. Doyle pers. comm.), young can briefly scatter from the nest prior to fledging. Few precocial birds feed their young after nest departure but other aspects of parental care such as vigilance may not be shared equally by the young. Food is provided to the young by American coots (*Fulica americana*) and other gallinules (Ehrlich et al. 1988) and vigilance increases with brood size in the southern lapwing (*Vanellus chilensis*; Walters 1982) and the bar-headed goose (*Anser indicus*; Schindler and Lamprecht 1987). The precocial young of these birds can scatter after hatch. In the above cases, the shared parental care hypothesis predicts that defence should increase with offspring number whereas the offspring mobility hypothesis predicts that defence should be unaffected.

Exclusive predictions can also be made if all aspects of parental care are shared equally among the young and the young cannot scatter. In both altricial and precocial birds, these conditions are met when parents defend eggs that are clumped in a nest. In this case, the offspring mobility hypothesis predicts that defence should increase with offspring number but the shared parental

care hypothesis predicts that defence should be unaffected.

Future research should focus on two areas. First, the effect of clutch size on egg production, incubation or other costs of past investment and the effect of brood size on recruitment should be measured for a wider range of birds. Study of those factors would support assumptions about past investment and future benefit in my and similar experimental designs (Sargent and Gross 1985). Second, any future comparisons of past investment and future benefit are valuable, given the paucity of well-controlled manipulative studies. In particular, offspring number should be manipulated in other stages of the nesting cycle for birds with different forms of parental investment and life histories.

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CHAPTER 3: BROOD DEFENCE TACTICS IN WILLOW PTARMIGAN: TESTS OF PARENTAL INVESTMENT THEORY

Introduction

Avian defence of young has provided a useful model for developing and testing parental investment theory. Most studies have used altricial birds (Montgomerie and Weatherhead 1988) although several precocial shorebirds have been examined recently (Reid and Montgomerie 1985; Byrkjedal 1987, 1989; Brunton 1990). Willow ptarmigan have been particularly well-studied precocial bird and are one of the few birds for which defence can be compared among different populations.

Several features of brood defence in willow ptarmigan are different from the patterns of avian defence described for other birds. First, annual variation in ptarmigan defence has been commonly observed, possibly as a function of changes in breeding density (Pedersen and Steen 1985; Pedersen 1989) or predation pressure (Hudson and Newborn 1990). Second, willow ptarmigan defence has not been observed to change with offspring age (Pedersen and Steen 1985; Hudson and Newborn 1990). Most studies of other birds have found some change in defence with offspring age (Montgomerie and Weatherhead 1988) with few exceptions (Hobson et al. 1988; Westmoreland 1989).

Four hypotheses have been suggested to explain why defence changes with offspring age. Changes in defence may be an artifact of repeatedly exposing parents to the same stimulus (Knight and Temple 1986b). Alternatively, parents may increase defence if opportunities for other reproduction decline as a breeding season progresses (Barash 1975). The reproductive value of young also increases with offspring age, not as a function of cumulative past investment, but because the future expectancy that the young will reach independence increases with their probability of survival (Andersson et al. 1980). The vulnerability of the offspring may decline after they leave the nest if they can escape and hide from predators.

Characteristics of the parents may also influence avian defence. For example, parents in poor body condition may give lower defence if aggressive defence is energetically costly (eg. Wallin 1987). If survival between breeding seasons is high and predictable, young parents could have a high residual reproductive value (Pianka and Parker 1975) and should invest less in risky defence (Pugesek 1983). Sexual dimorphisms in size or plumage may predispose either males (Wiklund and Stigh 1983; Andersson and Wiklund 1987; Wiklund 1990) or females (Hobson et al. 1988) towards stronger defence. A parent's certainty of parentage may vary with intraspecific nest parasitism or kleptogamy and this could also affect defence.

I examined brood defence in willow ptarmigan (*Lagopus l. alexandrae*) to evaluate which factors had the greatest influence on parental investment.

Methods

Study Animal and Area. The willow ptarmigan is a subalpine grouse with a circumpolar distribution. Birds usually form monogamous pairs but 5-20% of the males may pair with two females (Hannon and Martin 1991). Males are slightly larger and have wings that are 5-6% longer than those of females (Gruys 1991). Both the female and male have cryptic plumage during brood rearing, but the male's brown plumage is less patterned and darker. Females lay clutches of 5-11 eggs in shallow scrapes on the ground. Mortality is greater for females than males during the breeding season but is the same for the sexes during winter (Gruys 1991). Females may renest if their first nest is lost, but only one brood is produced per season. The precocial young are brooded by the female after they leave the nest and are defended by both parents.

I conducted this study at the Chilkat Pass in northwestern British Columbia, Canada (59°50'N, 136°30'W) during the breeding seasons of 1989-1990. I have also included data collected by other observers during 1979-1981 and 1984-1988. The study area is covered by a mixture of willow (*Salix* spp.) and birch (*Betulosa glandulosa*) shrubs and has been described in detail elsewhere (Hannon 1984; Gruys 1991). Potential predators of chicks that were

observed on the study area include: red foxes (*Vulpes vulpes*), short-tailed weasels (*Mustela erminea*), mew gulls (*Larus canus*), northern harriers (*Circus cyaneus*), short-eared owls (*Asio flammeus*) and common ravens (*Corvus corax*). Foxes (Sonerud 1988) and northern harriers (Hik et al. 1986) have been observed killing grouse chicks and are probably important brood predators. Sightings of foxes, harriers and owls were recorded each year along with the amount of time spent in the field.

General Methods. Willow ptarmigan were captured with noosing poles and ground nets (Hannon 1983) in early spring before laying began. Each bird was banded with a unique color combination and sex was determined by plumage. Age was assessed by pigmentation patterns on the primary wing feathers (Bergerud et al. 1963). Prior to 1985, nests and broods were located by searching with dogs. From 1985 to 1990, females were collared with small (15-18 g, 3-4% of the female's body weight) radios in order to find nests and broods. Females were flushed from the nest three times during incubation and were checked otherwise with telemetry. Telemetry has been shown to have little effect on the reproductive biology (Lance and Watson 1977; Erikstad 1979; Schieck 1988) of willow ptarmigan. Investigator disturbance did not affect clutch predation (Hannon unpub. data). The chicks were captured at hatch and marked with patagial wing tags (Hannon et al. 1990). Offspring age was known for the majority of broods but I estimated age for some broods using wing length (Hannon unpub. data). I classed young that were 1-10 days old as *chicks* and young that were 11-20 days old as *fledglings*. Chicks escaped predators by running and hiding in dense undergrowth whereas fledglings could scatter further by flying on long, shallow trajectories.

Measuring Brood Defence Behavior. Brood defence behaviour was recorded in two ways in this study. Between 1979 and 1988, the stimulus was an observer approaching with a dog and trying to catch the chicks. The defence behaviour was ranked on a 6 point scale as follows: (0) No defence, bird flies out of sight without giving a display; (1) Very Weak, bird flies away and calls from distance;

(2) Weak, bird stays 20-30 m from observer and walks in alert posture while calling; (3) Moderate, bird stays 10-20 m from observer and runs trailing wings with head held low; (4) Active, bird stays 5 m from observer and feigns injury by flapping wings and shaking tail; (5) Very Active, bird strikes observer. Between 1979 and 1988, broods were checked on a semi-regular basis to estimate brood survival. Observer bias was minimized because the same observer standardized the ranking procedure each year with new observers and because the ranking procedure was simple.

In 1989 and 1990, two observers played a taped chick distress call for 3 minutes and continuously recorded three measures of defence behavior: postures, vocalizations and distance from the observers. Each observer focused on one parent. I subjectively estimated the parent's risk of predation in the behaviors. Risky behaviors were usually observed only at the start of an encounter but continued if the parent's defence was strong. Risky postures included wing dragging, shaking the body and flying in short, active hops. I considered vocalizing or remaining less than 5 m from the observer to be risky. I also scored the parents' defence on the 6 point scale as above in order to compare 1989 and 1990 to previous years.

To test if previous exposure to the observer affected parental defence, I disturbed broods at three different rates: every day, every second day and every fourth day. Defence behavior was recorded for all broods when they were 1,5,9 and 13 days old. To avoid bias, the observers switched which parent they recorded on alternate days. Brood size of first nests was manipulated as part of another study (Chapter 2), but broods of different size were balanced among the different disturbance rates.

Our activity simulated a natural predator because the parents perceived us to be a threat and behaved more aggressively than birds without broods. I observed no natural encounters between parents with broods and predators although three radio-tagged females were killed (two by foxes, one unknown) in 1989 and 1990 while attending their broods.

Statistical Analyses. I used nonparametric tests for statistical comparisons when the measure was a rank score or the underlying distribution was not normal. All tests were performed using procedures from SAS (SAS Institute, 1987). I had no *a priori* reason to predict direction in any comparison so all tests were two-tailed and considered significant at probability levels less than 0.05.

Results

I held the previous number of exposures and offspring age constant to test for effects of year, age of parent, male presence, male mating status and nest attempt on brood defence. I used only first encounters of broods that were 1-3 days old. Broods from first nests where the male was present were used in tests of year effects, age of parent and male mating status. Broods from first nests were used in tests of the effect of male presence.

Year Effects

There was no difference among years in the proportion of yearling females ($\bar{x}$=56.6%, χ^2=3.71, P>0.75), yearling males ($\bar{x}$=43.3%, χ^2=6.34, P=0.50) or polygynous males ($\bar{x}$=23.4%, χ^2=10.92, P>0.10) in the sample of birds that were observed. I pooled data from both age-classes and all males to test for year effects. I included defence scores from 1989-1990 to compare years.

Conditions may differ among years because both ptarmigan and predator density may fluctuate. Spring density of ptarmigan was approximately 40 pairs/km^2 in 1979-1981 but declined and remained stable at about 20 pairs/km^2 in 1984-1990. Sightings of foxes (0.4-6.1/100 hours afield), northern harriers (2.2-7.9/100 hours afield) and short-eared owls (0.4-6.0/100 hours afield) fluctuated among years. Predation rates of first nests varied from 22.8-77.3% among years.

There was no difference among years in the proportion of females (χ^2=14.4, P>0.10) or males (χ^2=14.8, P>0.05) giving high risk defence (a score of 4 or 5). The proportion of birds giving high risk defence was not correlated with spring density, predator sightings or rates of nest predation (Table III-1).

Table III-1. Spearman rank correlation statistics comparing the proportion of birds giving high risk defence with annual conditions (*n*=9-10 years).

Sex	Annual Condition	Correlation Coefficient	P
Females	Breeding Density	-0.58	0.077
	Foxes	-0.08	0.83
	Short-Eared Owls	-0.17	0.67
	Northern Harriers	0.48	0.19
	Predation of First Nests	0.22	0.58
Males	Breeding Density	-0.50	0.14
	Foxes	-0.03	0.93
	Short-Eared Owls	0.07	0.86
	Northern Harriers	0.55	0.12
	Predation of First Nests	0.32	0.41

Fox sightings were not correlated with rates of nest predation (r=-0.20, P=0.63). I pooled data from all years where I gave parents defence scores. I also pooled data from 1989 and 1990, because no measure of detailed defence was different between years (all cases, P>0.05).

Age Class of Parent

The age of the parent may affect defence either because of their prior experience or the value of their residual reproduction. In the sample of birds that were observed, there was no difference among male age-classes in the proportion of polygynous males ($\bar{x}$=25.9%, χ^2=0.46, P=0.50). I pooled data from all males to compare age classes. Age class of parent had no effect on any measure of defence for either females or males (Table III-2), thus in subsequent analyses I pooled data from different age classes for both sexes.

Male Presence and Male Mating Status

If defence of a brood is most effective when both female and male are present, an unaccompanied female may compensate by being more aggressive. There was no difference in the defence of lone and accompanied females (Table III-3) and in subsequent analyses, I pooled data from all females. Monogamous and polygynous males may differ in their certainty of paternity in the clutch but there was no difference in their defence (Table III-3). Thus in subsequent analyses, I pooled data from all males, regardless of their mating status.

Nesting Attempt

Willow ptarmigan may renest if they lose the first nest to a predator. Parents defending broods from first nests or renests may differ in body condition or the young may differ in reproductive value. There was no difference between the defence of birds defending first nests or renests (Table III-4). Our sample of birds defending renests was too small for further comparisons so in subsequent analyses I have included only birds defending broods from their first nesting attempt.

Table III-2. Mann-Whitney U-test statistics comparing the defence of yearlings and adults.

Sex	Measure of Defence	Sample Size Yrlgs	Adults	*U*	P
Females	Defence Score	63	52	0.38	0.54
	Postures			0.15	0.69
	Vocalizations	14	11	0.19	0.67
	Distance < 5 m			1.32	0.25
Males	Defence Score	46	67	2.12	0.14
	Postures			2.08	0.15
	Vocalizations	10	15	0.11	0.74
	Distance < 5 m			0.10	0.75

Table III-3. Mann-Whitney U-test statistics comparing the defence of accompanied and unaccompanied females and the defence of monogamous and polygynous males.

Measure of Defence	Sample Size Unacc.	Acc.	*U*	P
Defence Score	18	115	0.02	0.89
Postures			0.16	0.69
Vocalizations	5	25	0.64	0.42
Distance < 5 m			0.52	0.47

Measure of Defence	Sample Size Monog.	Polyg.	*U*	P
Defence Score	63	22	0.24	0.62

Table III-4. Mann-Whitney U-test statistics comparing the defence of parents with broods from first nests and renests.

Sex	Measure of Defence	Sample Size Nests	Renests	*U*	P
Females	Defence Score	133	26	1.66	0.20
	Postures			3.25	0.072
	Vocalizations	30	12	0.03	0.87
	Distance < 5 m			2.98	0.084
Males	Defence Score	115	16	1.12	0.29
	Postures			2.06	0.15
	Vocalizations	25	10	0.81	0.37
	Distance < 5 m			0.00	0.99

Rate of Disturbance

If birds are repeatedly disturbed, changes in defence that are correlated with offspring age may be obscured by positive reinforcement or habituation in the parent's behaviour. I examined the defence of birds that differed in past exposure at two points after hatch. For the birds that were given a defence score, previous exposure varied from 0-3 checks when the brood was 4-6 days old and from 0-4 checks when the brood was 8-10 days old. For the birds that I recorded detailed defence, previous exposure varied from 1-4 checks when the brood was 5 days old and 2-8 checks when the brood was 9 days old. A bird was included once in a given test. Past exposure to the observer had no effect on either female or male defence (Table III-5). In subsequent analyses, I pooled data from birds with different past exposure, but only for the range of previous checks that I tested.

Age of Offspring

To test the effect of age of offspring on brood defence for birds that I gave a defence score, I included two observations: one encounter with chicks and one with fledglings. The proportion of birds giving aggressive defence appeared to decline gradually with offspring age (Fig. III-1), but there were no differences in defence among birds with chicks or fledglings of different ages (Table III-6). However, both females (Wilcoxon paired-sample test, T=904, $P<0.001$) and males (T=800, $P<0.005$) gave stronger defence when they were defending chicks than when they were defending fledglings (Fig. III-1).

To test the effect of age of offspring on brood defence for birds that I recorded detailed defence, I included all observations of birds that were disturbed on alternate days (Fig. III-2) and were present for at least five of the seven possible encounters. There was no difference in the defence of birds defending chicks of different ages (Table III-6). I did not compare birds defending chicks and fledglings because I observed broods only twice after the young fledged. However, the time parents spent in high risk postures and close to the observers appeared to be lower after the young fledged (Fig. III-2).

Table III-5. Kruskall-Wallis statistics (χ^2 approximation) comparing the defence of parents with different numbers of previous encounters with the observers. Two brood ages are considered: 4-6 and 8-10 days after hatch.

4-6 Days After Hatch

Sex	Measure of Defence	Sample Size # of Checks 0	1	2	4	χ^2	P
Females	Defence Score	70	47	19		1.04	0.59
	Postures					1.92	0.38
	Vocalizations		9	7	6	1.50	0.47
	Distance < 5 m					0.57	0.75
Males	Defence Score	60	37	16		0.47	0.79
	Postures					2.32	0.31
	Vocalizations		7	3	5	0.69	0.71
	Distance < 5 m					0.98	0.61

8-10 Days After Hatch

Sex	Measure of Defence	Sample Size # of Checks 0	1	2	3	4	8	χ^2	P
Females	Defence Score	32	39	30	15			4.07	0.25
	Postures							0.36	0.84
	Vocalizations			9		7	6	0.18	0.91
	Distance < 5 m							2.75	0.25
Males	Defence Score	31	33	26	14			3.00	0.39
	Postures							4.96	0.08
	Vocalizations			7		3	5	2.76	0.25
	Distance < 5 m							0.57	0.75

Fig. III-1. The proportion of rank scores versus offspring age. The ptarmigan young fledged between 9 and 11 days after hatch. Two observations were included for each brood, one before this point and one after. Each bar contains scores that are pooled for a two day interval with the sample size on top. Symbols for the rank scores are: 0 □; 1-2 ▨; 3 ▨; 4 ▨; and 5 ■.

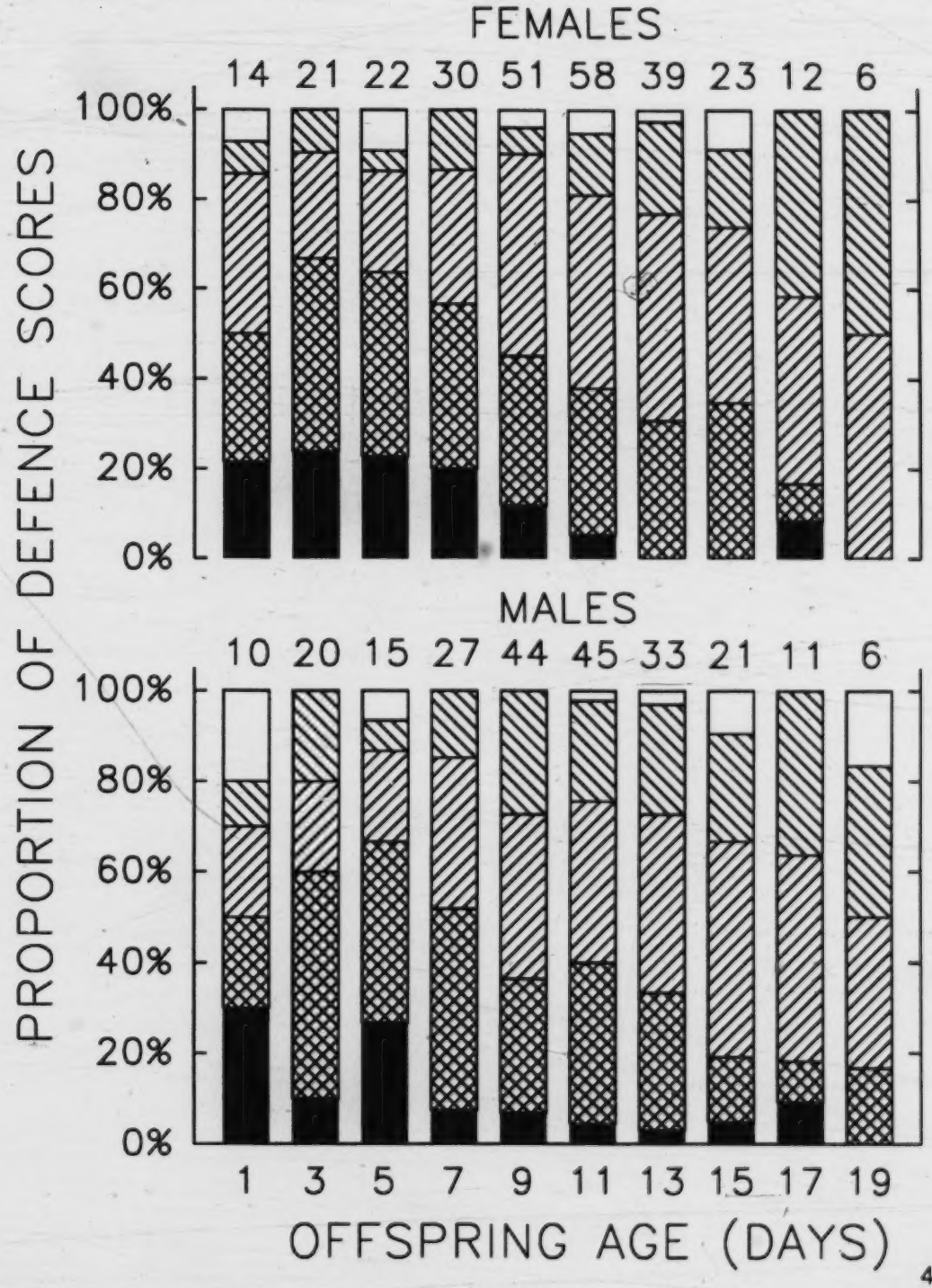
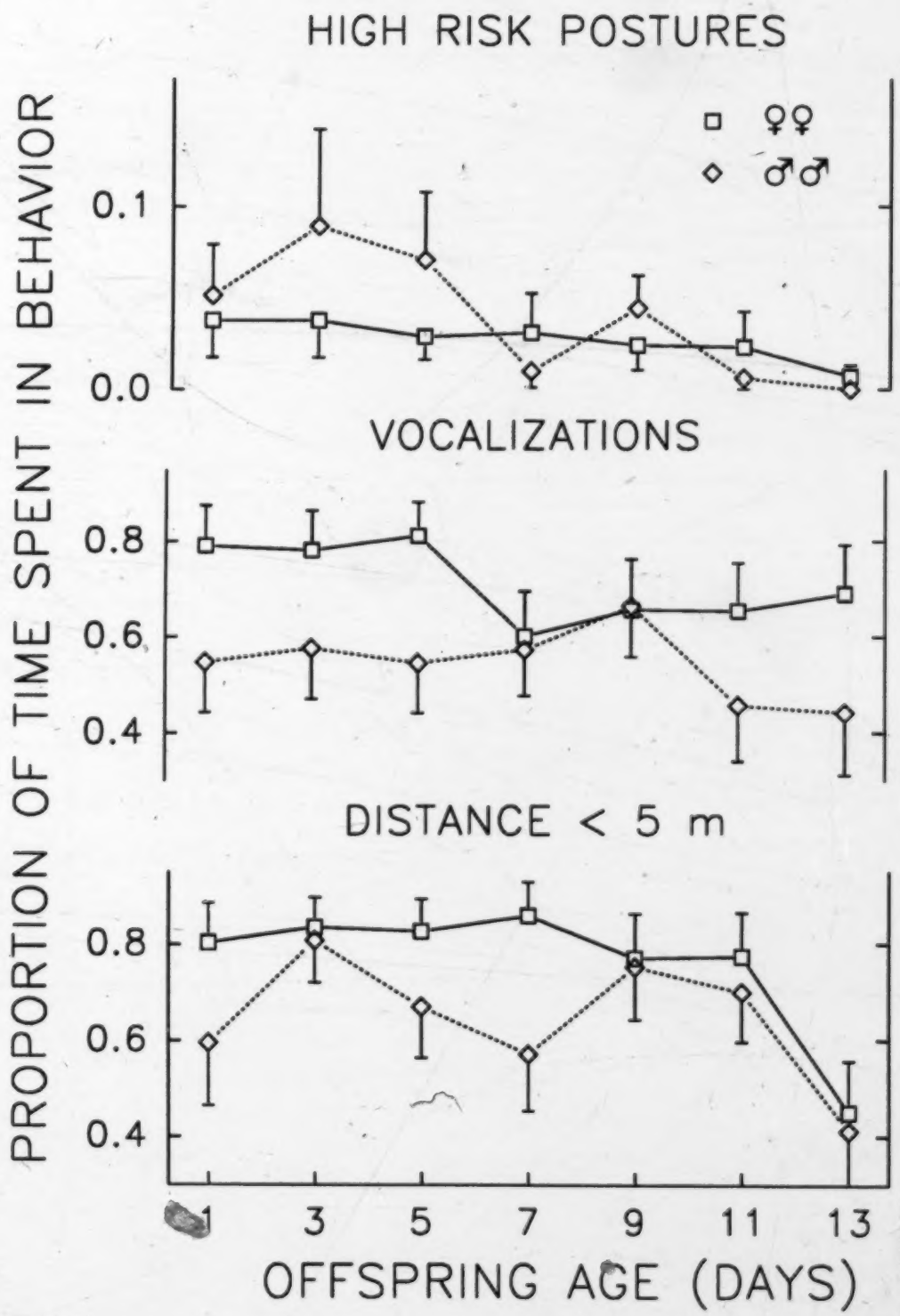

FEMALES
14 21 22 30 51 58 39 23 12 6
100%
80%
60%
40%
20%
0%
MALES
10 20 15 27 44 45 33 21 11 6
100%
80%
60%
40%
20%
0%
PROPORTION OF DEFENCE SCORES
1 3 5 7 9 11 13 15 17 19
OFFSPRING AGE (DAYS)

Table III-6. Kruskall-Wallis (χ^2 approximation) statistics comparing the defence of parents with different aged chicks or fledglings. For sample sizes, see Figs. 1 and 2.

Among Chicks of Different Ages Sex	Measure of Defence	χ^2	P
Females	Defence Score	3.07	0.55
	Postures	1.12	0.89
	Vocalizations	4.77	0.31
	Distance < 5 m	0.73	0.95
Males	Defence Score	5.26	0.26
	Postures	3.10	0.54
	Vocalizations	1.20	0.88
	Distance < 5 m	4.67	0.32

Among Fledglings of Different Ages Sex	Measure of Defence	χ^2	P
Females	Defence Score	5.40	0.25
Males	Defence Score	5.21	0.27

Fig. III-2. The proportion of time spent in defence behavior versus offspring age. The ptarmigan young fledged between 9 and 11 days after hatch. Five to seven observations were included for each parent. Sample size of parents: females n=19; males n=16. Each point is a $\bar{x}\pm$1SE and contains observations for one day.


HIGH RISK POSTURES
♀♀
♂♂
0.1
0.0
VOCALIZATIONS
0.8
0.6
0.4
DISTANCE < 5 m
0.8
0.6
0.4
PROPORTION OF TIME SPENT IN BEHAVIOR
1
3
5
7
9
11
13
OFFSPRING AGE (DAYS)

Sex of Parent

I compared sexes as paired samples because parents may influence eachother's defence. I pooled data from birds defending chicks and data from birds defending fledglings. Females had higher defence scores than males while defending chicks (Wilcoxon paired-sample test, T=317, P<0.001) although the difference was not significant while the pairs defended fledglings (T=575, P>0.10). There was a trend for males defending chicks to spend more time in high risk postures (Fig. III-2, T=205.5, P>0.20) but females spent more time vocalizing (T=306.5, P<0.001) and at distances less than 5 metres (T=194, P<0.005).

Individual Variation

Defence may have been affected by an intrinsic quality of the parent that I did not measure. To examine individual variation in brood defence, I used observations of birds defending unfledged chicks. I compared the first and second encounter within a year or the two first encounters in different years. Individual defence was correlated positively within (Spearman rank correlation, ♀♀ r=0.53, P<0.0001, n=127; ♂♂ r=0.48, P<0.0001, n=104) and between years (♀♀ r=0.33, P=0.09, n=27; ♂♂ r=0.56, P=0.005, n=24). Repeated observations of birds in different years were uncommon and formed only 0-10% of the samples in above tests.

Discussion

Several results in this study are not consistent with previous studies of brood defence by willow ptarmigan in Norway (*Lagopus l. lagopus*, Pedersen and Steen 1985) and red grouse in Scotland (*Lagopus l. scoticus*, Hudson and Newborn 1990). I found no annual variation in ptarmigan defence although both of the previous studies described annual changes in the proportion of birds giving defence. I found that defence declined after ptarmigan young had fledged but neither of the previous studies found any change in defence with offspring age. Two differences may partially account for these contrasting observations.

First, some of the factors that I considered separately appear to have been pooled in the previous studies. This may have affected their conclusions. For example, if willow ptarmigan or red grouse in Europe had defended renests strongly and the number of renests had varied among years, pooling defence data from different nesting attempts could have produced spurious annual variation. Second, willow ptarmigan in Europe are less aggressive in defence than birds in British Columbia. In Europe, 20-70% of ptarmigan gave no defence (Pedersen and Steen 1985; Hudson and Newborn 1990), compared to only 0-20% of the ptarmigan in this study (Fig. III-1). This striking difference is likely a product of past human exploitation throughout the continuously inhabited areas of Europe. High levels of predation pressure in the past may have selected for less aggressive ptarmigan. In any case, changes in defence with offspring age or other factors could be obscured if few birds are aggressive.

Annual Variation in Brood Defence

Breeding Density. Ptarmigan defence was not correlated with the spring breeding density of birds in our study area, but Pedersen and Steen (1985) found a positive trend for males to give more displays in years of high density. Pedersen and Steen (1985) suggested that parent quality may have been important but breeding density could also affect defence if competition for food affected ptarmigan nutrition. In Scotland, managed red grouse populations can reach densities two to threefold greater than our highest observed density (Hudson 1986). Breeding density should have a greater effect on parental nutrition in Scotland but Hudson and Newborn (1990) found that experimentally improved body condition did not affect the proportion of ptarmigan giving defence. The ptarmigan population in our study area may not reach numbers that could negatively affect nutrition.

Predation Pressure. Ptarmigan defence was not correlated with annual variation in fox sightings in our study area, although Hudson and Newborn (1990) found that the number of birds performing risky displays was correlated

positively with the number of fox dens destroyed in the spring. Hudson and Newborn (1990) suggested that red grouse monitor predation pressure prior to laying but it is unclear why grouse would base defence on past predation pressure. If the gamekeepers missed some fox dens, predation pressure could have been high during brood rearing.

In this study, predator sightings and nest predation were not correlated with brood defence. However, these variables may have been poor measures of predation pressure. Fox sightings were not correlated with nest predation and the availability of other prey may have changed during brood rearing. For example, arctic ground squirrels (*Spermophilus parryi*) are an important component in the diet of fox kits in our area (Jones and Theberge 1983), and the emergence of juvenile squirrels often coincides with hatch of first nests. As well, predation on nests is lower late in the breeding season (Martin and Hannon submitted). There may have been no annual fluctuations in ptarmigan defence because predation pressure during brood rearing was similar for all years.

Intrinsic Quality of the Parents. Avian defence is often highly variable (Regelmann and Curio 1983; Montgomerie and Weatherhead 1988), but I found little individual variation in willow ptarmigan brood defence. If avian defence is affected by intrinsic qualities of the parent, pooling repeated observations of the same birds in different years could reduce annual variation in defence. However, annual survival and nest success of ptarmigan were low in this study, and only a few parents successfully hatched a brood in more than one year. Pooling repeated observations cannot explain why there were no annual fluctuations in brood defence.

Changes in Brood Defence with Offspring Age

Parental investment in brood defence may change with offspring age as a function of the parent's past exposure to the predator, the potential for other nesting attempts or the reproductive value and vulnerability of the offspring.

Past Exposure to the Predator. Researchers have used three approaches to

show that past experience with a predator or model does not affect avian defence of young. First, some birds produce multiple broods in one breeding season. Defence increases and declines with offspring age during each nesting attempt, even though the cumulative number of past exposures increases (Greig-Smith 1980; Weatherhead 1989). Second, naive birds defending nests have been compared with young of different ages. Birds defending older offspring still usually have stronger defence (Stephen 1963; Röell and Bossema 1982; Andersen 1990, but see Hobson et al. 1988). Third, birds with different amounts of past exposure have been compared while defending young of the same age. Studies using this approach have found little (Breitwisch 1988) or no (Redondo and Carranza 1989; Weatherhead 1989; Westmoreland 1989; Westneat 1989; Rytkönen et al. 1990; this study) evidence of either positive reinforcement or habituation in the parents' defence.

Knight and Temple (1986a; 1986b) found evidence of positive reinforcement and suggested that weak initial defence could allow a parent to measure a predator's threat. In the case of habituation, weak defence could allow a parent to avoid a familiar risk. However, past exposure should not affect avian defence if the cost of weak defence is high. Thus, if the cost of weak defence for ptarmigan is total brood loss, a parent should treat each predator encounter as novel and give strong defence. Sonerud (1988) suggested that grouse should give weak defence if defence cues predators to search for the brood, but this tactic should only be important if grouse encounters with experienced predators are frequent.

Potential for Other Nesting Attempts. Barash (1975) suggested that defence should increase with offspring age because a parent's ability to replace a depredated clutch declines as the breeding season progresses. This explanation can be rejected for willow ptarmigan and some other arctic nesting birds (Reid and Montgomerie 1985). If a clutch is depredated after mid-incubation, a female willow ptarmigan will not lay another nest in the same breeding season (Martin and Hannon unpub. data). Once a clutch has

hatched, the brood will be the parent's only reproductive attempt in a season. This may explain why birds defending broods from first nesting attempts and renests did not differ in defence.

Reproductive Value of Offspring. In our study area, rates of predation on ptarmigan eggs can be very high but total loss of all the chicks in a brood is uncommon (Martin et al. 1989). Thus, the reproductive value of the brood probably increases with offspring age after ptarmigan young leave the nest. If older young had greater reproductive value, defence intensity should increase after the young hatch, but parental defence did not increase with chick age and declined after the young fledged. Changes in the reproductive value of the young with offspring age appear to have little effect on defence after nest departure.

The reproductive value of offspring may also vary for different nesting attempts and brood sizes. Ptarmigan young from first nests recruit to the breeding population more often than young from renests (Martin and Hannon 1987). Although young from first nests had a higher reproductive value, there was no difference between birds defending broods from different nesting attempts. A brood's reproductive value should also increase with offspring number but brood size has no effect on ptarmigan defence (Chapter 2).

Vulnerability of Offspring. The decline in ptarmigan defence with offspring age is consistent with changes in offspring vulnerability after nest departure. There was no difference among parents defending chicks of different ages although the ability of willow ptarmigan chicks to maintain homeothermy (Aulie 1976) and spend time away from the female increases with age (Boggs et al. 1977; Pedersen and Steen 1979). However, both female and male defence declined after the young fledged at 9-11 days of age. Thus, the ability to thermoregulate may not give young escaping predators as great an advantage as being able to fly. Flight should be especially important in helping juvenile ptarmigan escape ground-based predators such as the red fox. The defence of other precocial birds also declines with offspring age after the young have left the nest

(Stephen 1963; Brunton 1990).

Variation in Brood Defence Between and Within the Sexes

The defence of female willow ptarmigan was stronger than males in this study and in previous studies (Pedersen and Steen 1985; Hudson and Newborn 1990). Differences between and within the sexes in body condition, future reproduction, plumage and certainty of parentage may affect parental investment in brood defence.

Body Condition. I did not measure body condition of birds but inferential evidence suggests that body condition does not limit ptarmigan defence. The timing of molt may reflect a bird's body condition because molt and replacement of primary wing feathers can be energetically costly (Blem 1990). Male willow ptarmigan usually begin molting while their mate is incubating a first nest whereas female willow ptarmigan delay molt until they are no longer incubating (Hannon unpub. data). Thus, males defending broods from renests should be in better condition than males defending broods from first nests, and all males should be in better condition than females. As well, females defending broods from renests may be in worse condition because they have laid a previous clutch. However, there was no difference between birds defending broods from different nesting attempts and female defence was consistently stronger. Body condition would not be important if ptarmigan defence has inexpensive energy demands. Ptarmigan defence is often of short duration and the parents usually run on the ground while the young scatter quickly. A parent's risk of predation during defence is probably a greater potential cost than any energy expenditure.

Future Reproduction. Birds should invest more in defence of current offspring if annual mortality is high and they have little residual reproduction (Pianka and Parker 1975). Return rates can be used as a measure of annual mortality but may be confounded by territory switching. In willow ptarmigan, return rates are lower for females than males (Gruys 1991) and few birds move more than one territory between years (Schieck and Hannon 1989). Female willow ptarmigan

should have less residual reproduction and strong female defence is consistent with age-specific reproductive tactics. However, return rates are low for both sexes (♀♀ $\bar{x}$=44.1; ♂♂ $\bar{x}$=52.5, n=8 years, Gruys 1991) and there was no difference in defence between age-classes in either sex. Residual reproduction is probably low for all willow ptarmigan and should not affect their defence tactics. Most studies have not found age-specific defence tactics in birds (Breitwisch 1988; Hobson et al. 1988; Wiklund 1990; but see Pugesek 1983), probably because most birds are short-lived and have uncertain future reproduction.

Plumage. Differences in plumage may explain patterns in defence between the sexes. If the male is more conspicuous and attracts a predator's attention because of his dark plumage, he would be at greater risk than a female. Thus, males may have to vocalize less and stay further from the observers than females to reduce their risk. Size and plumage dimorphism may not generally account for differences in female and male defence, however, because in some monomorphic species one sex often gives stronger defence (eg. Weatherhead 1979, Regelmann and Curio 1986) while in some dimorphic species there is no difference between the sexes (Greig-Smith 1980).

Certainty of Parentage. Certainty of maternity is high among female willow ptarmigan because intraspecific nest parasitism is rare (Martin 1984a; Hannon unpub data). However, certainty of parentage should vary between the sexes and among male ptarmigan. Extra-pair copulations have been observed in willow ptarmigan (Martin and Hannon 1988) and male rock ptarmigan (*Lagopus mutus*) seek additional matings on neighbour's territories (Brodsky 1988). In a forced choice experiment, Martin (1984b) showed that male willow ptarmigan switch their defence priority from their mate to their offspring at mid-incubation, possibly because they risk no loss of paternity after this point. Polygynous males may have a lower certainty of parentage than monogamous males as they share their mate guarding between two females (Hannon and Martin 1991) but I found no difference in defence between males with one or two females.

Stronger female defence in willow ptarmigan is consistent with the expectation that males have a lower certainty of parentage than females.

Future Research

Vulnerability of the young, parental plumage and parental certainty of parentage appear to be the most important factors affecting brood defence in willow ptarmigan. In this study, I used an inferential approach to evaluate the factors affecting defence but manipulative experiments may be a stronger approach in the future. For example, moving broods of different ages between pairs would test the importance of offspring vulnerability. Parents should give weaker defence if an older brood is transferred to them. Manipulations of plumage with dyes could change the risk of predation for female and male ptarmigan. If parents are able to perceive the changes in their plumage, they should alter their defence tactics to minimize their risk of predation. New techniques such as DNA fingerprinting could be used to examine parentage in the clutch. On the basis of strong female defence, I would expect that some clutches would have mixed paternity. The above are only a sample of possible tests, and researchers could develop additional approaches to further examine the factors affecting avian defence.

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CHAPTER 4: THESIS DISCUSSION

The measurement, analysis and function of avian defence behavior

The understanding of patterns in avian defence behavior may be confused by two problems. First, the methodology used in the measurement and analysis of defence behavior may have a substantial effect on any conclusions. Second, additional variability may be introduced into measurements of behavior if defence of offspring has functions in other contexts.

The selection of an appropriate predator model may be important. Birds have been shown to give separate levels of defence to different natural (Greig-Smith 1980; Buitron 1983) or model (Patterson et al. 1980; Knight and Temple 1988; but see Knight and Temple 1986) predators. In this study, brood defence was directed towards a human observer. However, a human may not be comparable to a bird's natural predators (Montgomerie and Weatherhead 1988). Parents did not always react to the approach of the observer but the distress call of a chick was a strong stimulus for defence. Thus, although my activity probably did not resemble fox or raptor behavior, a predation event would have been simulated if ptarmigan young call when threatened by natural predators.

Defence is often measured as a rank score (Andersson et al. 1980; Blancher and Robertson 1982; Röell and Bossema 1982; Wiklund and Stigh 1983; Wallin 1987; Weatherhead 1990), probably because ranking procedures are simple and easy to replicate among observers. A comprehensive ethogram of willow ptarmigan behavior has been available for some time (Watson and Jenkins 1964), but previous studies have used a simple rank score to describe ptarmigan defence of offspring (Hannon 1984; Pedersen and Steen 1985; Martin 1989; Pedersen 1989; Hudson and Newborn 1990). By recording detailed observations, I was able to describe sexual differences in defence with greater resolution (Fig. III-2). Researchers should consider recording defence in greater detail in future studies.

There are some subtle problems in the statistical analysis of defence behavior. If repeated observations of the same individual are treated as

independent, the degree of freedom is inflated, which may increase the likelihood of a Type I error (Westmoreland 1989). This was not the case in my study. In tests of the effect of offspring age, I included repeated observations where I recorded detailed defence (Fig. III-2), but the observations were independent where parents were given a rank score (Fig. III-1). The results of both analyses were consistent: chick age had no effect on parental defence (Table III-6). The power of statistical tests is low if sample size is small, which may increase the likelihood of a Type II error (Zar 1984). For example, the proportion of time that females spent close to the observers was significantly higher than males in a large sample in Chapter 3 but not in a smaller sample in Chapter 2. However, I assumed that the sample size was robust enough to show differences in all tests. If I have committed Type II errors, future research with larger samples of ptarmigan or other birds may yield different conclusions.

Defence of offspring may have functions in other contexts. Parents may share investment in defence if their collateral kin will benefit or if they expect some reciprocal benefit (Shields 1984). However, shared defence should only be important in birds that nest at high densities or in colonies and would not affect the parental defence of dispersed ptarmigan broods. While defending their young, males may also be defending their mate. Males may use defence to advertise their quality to a mate (Curio 1980) or to protect their paternity in subsequent breeding attempts in the same season (Martin 1984). These factors should not affect brood defence by male willow ptarmigan because they have only one reproductive attempt in a season.

Defence by a male may also enhance the survival of his mate to following breeding seasons. Male investment that enhances female survival would be particularly advantagous if the sex-ratio of the population is male-biased (Breitwisch 1988) or if female survival outside of the breeding season is high. Pairing with a previous mate is advantagous for male willow ptarmigan reproductive success (Schieck and Hannon 1989) but male accompaniment has no effect on female return rates (Martin and Cooke 1987; Hannon and Martin

1991). As well, the ptarmigan sex ratio is usually even (Hannon 1983, 1984) and few ptarmigan have a familiar partner return (Schieck and Hannon 1989).

Significance of this study

I used a novel experimental design in Chapter 2 to separate the effects of past investment in the clutch and the future benefit of brood size. My experimental design was an extension of suggested methodology (Sargent and Gross 1985) that has largely been untested. One previous study has measured the effects of past investment and future benefit on defence of offspring (Coleman et al. 1985) and found that both factors affected defence. My results were quite different: neither past investment nor future benefit affected willow ptarmigan defence of young. Similar studies have often assumed that past investment increases with clutch size (eg. Weatherhead 1979) and that future benefit increases with brood size (eg. Wiklund 1990). These important assumptions are rarely tested (Coleman and Whitall 1988). Although I did not find a cost of incubation, past investment in egg production costs likely increased with clutch size. I showed that brood size at hatch was a good predictor of future benefit.

Many variables affect defence behavior (Montgomerie and Weatherhead 1988) and other studies of willow ptarmigan have considered only a few (Pedersen and Steen 1985; Hudson and Newborn 1990). I was able to test additional factors more rigorously because radio telemetry allowed me to track mobile broods and collect systematic data on defence behavior. In general, my conclusions should be stronger than those of previous work.

Defence of offspring by precocial birds

Most studies of avian defence have used altricial birds (Montgomerie and Weatherhead 1988) and studies of defence in precocial birds have been previously neglected, possibly for logistical reasons. However, these studies are useful on a comparative basis and by contrasting the defence of willow ptarmigan with altricial birds, I have been able to suggest explanations that could have broad application in understanding patterns of avian defence.

Offspring number and age may affect the defence of altricial and

precocial birds in different ways. I showed in Chapter 2 that ptarmigan did not increase their investment in defence if I manipulated brood size, although defence increases with offspring number for most altricial birds. I have suggested three testable hypotheses which may be useful in guiding future research. Different predictions have also been made for altricial and precocial birds defending unfledged chicks. Several studies (Andersson et al. 1980; Montgomerie and Weatherhead 1988; Brunton 1990) have predicted that the defence of altricial birds should increase with offspring age whereas the defence of precocial birds should decline. I showed in Chapter 3 that ptarmigan defence declined, possibly because the vulnerability of the young has a greater effect than the reproductive value of the young.

In conclusion, brood defence by willow ptarmigan did not match the expected patterns in several cases. For example, parental investment in defence was not affected by brood size. Contrary to previous work on willow ptarmigan in other areas, brood defence of birds in the Chilkat Pass showed no evidence of annual fluctuations and declined in intensity with offspring age. As further research proceeds on other populations of willow ptarmigan and other birds, workers may continue to describe unexpected and interesting patterns of parental investment in defence.

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